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Resin secretory structures of *Boswellia papyrifera* and implications for frankincense yield

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• *Background and Aims* Frankincense, a gum-resin, has been tapped from *Boswellia papyrifera* trees for centuries. Despite the intensive tapping and economic interest of *B. papyrifera*, information on the resin secretory structures, which are responsible for synthesis, storage and transport of frankincense, is virtually absent. This study describes the type, architecture and distribution of resin secretory structures of *B. papyrifera* and its relevance for the ecophysiology and economic use of the tree.
• *Methods* The type and architecture of resin secretory structures present in bark and wood was investigated from transversal, tangential and radial sections of bark and wood samples. The diameter and density (number of resin canals mm^{-2}) of axial resin canals were determined from digital images of thin sections across the different zones of inner bark.
• *Key Results* Resin canals form a three-dimensional network within the inner bark. Yet, the intact resin-conducting and producing network is on average limited to the inner 6·6 mm of the inner bark. Within the inner bark, the density of non-lignified axial resin canals decreases and the density of lignified resin canals increases from the vascular cambium towards the outer bark. In the wood, only radial resin canals were encountered.
• *Conclusions* Frankincense tapping techniques can be improved based on knowledge of bark anatomy and distribution and architecture of resin secretory structures. The suggested new techniques will contribute to a more sustainable frankincense production that enhances the contribution of frankincense to rural livelihoods and the national economy.

Key words: *Boswellia papyrifera*, frankincense, resin secretory structures, resin canal, bark anatomy, tapping.

INTRODUCTION

Resin is considered to be the most versatile material in the pre-industrial world (Langenheim, 2003). Resins from *Boswellia* and *Commiphora* species (respectively known as frankincense and myrrh) were traded as incenses from the southern coast of Arabia to the Mediterranean region and Mesopotamia for more than a millennium (Groom, 1981; Gebrehiwot *et al.*, 2003; Langenheim, 2003). Their historical value is illustrated by the gifts of the three kings (frankincense, myrrh and gold) to Jesus Christ (Matthew 2: 11). Currently, the main international trade is from *Boswellia papyrifera*, and Ethiopia is the main exporting country (Coppen, 2005). The use of frankincense for ritual purpose in Ethiopia dates back to the Aksumite Empire, approx. 500 BC (Goldschmidt, 1970). The current commercial harvest of frankincense from this species provides an important export item and is a source of income for rural households in northern Ethiopia (Gebrehiwot *et al.*, 2003; Lemenih and Teketay, 2003; Tadesse *et al.*, 2007; Lemenih *et al.*, 2007). In some areas collection of resin is economically a more attractive land use than crop production and accounts for the majority of income of rural households (Tilahun *et al.*, 2007; Woldeamanuel, 2011; Dejene *et al.*, 2012). Modern uses of frankincense include church ceremonies, perfume and medicine production (Gebrehiwot *et al.*, 2003; Lemenih and Teketay, 2003).

Frankincense is produced by wounding the bark of *B. papyrifera* trees and collecting the resin that is subsequently released from the wound. This tapping practice is carried out at several spots along the stem, using a traditional type of axe. This procedure is repeated in 8–12 tapping rounds during the dry season which lasts about 8 months. The wound initially has a surface area of about 2·5 cm^2 and a depth of about 1 mm (Tadesse *et al.*, 2004). At each tapping round, the hardened resin is removed and the tapping wound is re-opened and enlarged. The number of tapping spots on each tree depends on the diameter of the tree. In the past, trees were tapped with 6–12 tapping spots around the stem (Ogbazghi, 2001; Gebrehiwot *et al.*, 2003). Currently, due to the high demand for frankincense, up to 27 tapping spots are made per tree in some commercial sites (Kebede, 2010). Frankincense yield per tree levels off after nine tapping spots (Eshete *et al.*, 2012*a*). Frankincense yield per tree per season varies between 41 and 3000 g depending on tree size, site productivity and season, and the yield increases during the earlier tapping rounds after which it levels-off and ultimately decreases towards the end of the dry season (Eshete *et al.*, 2012*a*; Tilahun *et al.*, 2011).

Extraction of resin through tapping likely affects carbohydrate allocation in trees as it enhances the competition for assimilates (Herms and Mattson, 1992; Rijkers *et al.*, 2006; Silpi *et al.*, 2007; Mengistu, 2011; Mengistu *et al.*, 2012). Resin extraction also induces mechanical damage to the trees (Herms and Mattson, 1992). Silpi *et al.* (2006) found 80 % reduction in radial growth in tapped trees compared with untapped trees in rubber wood (*Hevea brasiliensis*). Higher mortality of tapped adult trees was also reported for black dammar (*Canarium strictum*) by Varghese and Ticktin (2008). For *B. papyrifera,* tapping reduced reproductive effort and seed size (Rijkers *et al.*, 2006): tapped trees produced fewer flowers, fruits and seeds than non-tapped trees, and germination success of the seeds from non-tapped trees was much higher than from tapped trees (Eshete *et al.*, 2012*b*). Tapping also reduced foliage production, annual carbon gain and carbon stock of *B. papyrifera* trees (Mengistu, 2011; Mengistu *et al.*, 2012). Such negative effects could, at least partly, explain the recent lack of regeneration observed for *B. papyrifera* populations in northern Ethiopia (Lemenih *et al.*, 2007; Negussie *et al.*, 2008; Abiyu *et al.*, 2010; Groenendijk *et al.*, 2012).

Resin is produced by trees to protect against potential damage from abiotic or biotic stress (Lewinsohn *et al.*, 1990; Langenheim, 1995; Trapp and Croteau, 2001; Baier *et al.*, 2002; Pickard, 2008). Depending on the type of species, resin may be accumulated in resin canals or resin pockets (blisters) (Nagy *et al.*, 2000; Langenheim, 2003) in the wood and/or the bark (Fahn, 1988; Nussinovitch, 2010). In some species, tangential rows of traumatic resin canals are induced after wounding (Berryman, 1972; Fahn, 1979; Nagy *et al.*, 2000; Martin *et al.*, 2002). Resin canals (axial or radial) are elongated extracellular structures, which enable long-distance resin transport, while resin pockets are rounded intracellular isolated tissues with limited potential for resin transport (Langenheim, 2003). Resin secretory structures are formed by schizogeny or lysigeny. Lysigeny refers to the process of cell disintegration that occurs when new structures are differentiated with or without cell separation while schizogeny refers to formation of space by pulling apart of cells (Nair and Subrahmanyam, 1998; Pickard, 2008). In both cases, resin is produced by secretory cells known as 'epithelium' (Esau, 1965; Fahn, 1979; Wiedenhoeft and Miller, 2002; Kolalite *et al.*, 2003) which surrounds resin canals or resin pockets (Nair and Subrahmanyam, 1998; Wiedenhoeft and Miller, 2002; Langenheim, 2003). In some plants, the epithelial cells may become thick walled and lignified and become non-functional, while in others these cells remain thin walled, unlignified and functional for longer periods of time (Bannan, 1936; Langenheim, 2003).

Despite the intensive tapping and economic interest in frankincense production, information on the resin secretory structures of *B. papyrifera* is absent. This is the first study that both describes and quantifies the resin secretory structures in the bark of frankincense trees of *B. papyrifera*. After a bark incision a copious amount of white incense immediately oozes out. Hence we would expect the resin secretory structures of *B. papyrifera* to be abundant in the bark rather than in the xylem. We also hypothesized that density of axial resin canals show directional changes throughout the bark due to dilatation (Junikka, 1994; Kolalite *et al.*, 2003). Tadesse *et al.* (2004) indicated high variations in frankincense yield among trees of the same size classes. Studies indicate that the most important resin canal trait that determines resin yield for Norway spruce and pine trees is the diameter of resin canals (Baier *et al.*, 2002). This leads to the expectation that the diameter of resin canals in *B. papyrifera* varies among trees of the same size. This information is crucial to understand resin yield and will help to formulate recommendations for developing a more sustainable tapping regime.

MATERIALS AND METHODS

Study species

Boswellia papyrifera produces the widely traded white incense and is distributed in Ethiopia, Eritrea, Nigeria, Cameroon, Central African Republic, Sudan, Chad and north-east Uganda (Vollesen, 1989). In Ethiopia, *B. papyrifera* grows in dry Combretum–Terminalia woodlands and wooded grasslands in the north (Bekele *et al.*, 1993). It is a deciduous tree that usually dominates on steep and rocky slopes, lava flows or sandy valleys and grows to a height of about 12 m (Vollesen, 1989; Bekele *et al.*, 1993).

Study site

The study area is located near the village of Lemlem Terara, Metema district, northern Ethiopia (12 °39′ to 12 °45′N, 36 °17′ to 36 °23′E). The samples were collected from trees growing in open woodland located at 870 m a.s.l. Based on data from National Meteorological Agency of Ethiopia, for the period 1971–2009, annual rainfall in Metema ranges from 665 to 1380 mm, with a mean annual rainfall of 960 mm. The major rainy season in the site is from June to September. The mean annual maximum and minimum temperatures are 36 °C and 19 °C, respectively. The study site is dominated by clay soil and its average soil depth is 27·7 cm (Eshete *et al.*, 2011).

Study trees, sampling and sample preparation

The field-data collection was done in February 2010, in the middle of the dry season. Twenty healthy looking, adult trees of about 10 m height with a straight stem and diameter at breast height between 20 and 25 cm were selected from the same site in Metema. Trees without traces of recent tapping were selected. Non-tapped trees were used since the objective of this study is to describe the basic structure of resin secretory structures of the species. One bark sample per tree was collected from the eastern side at breast height (1·3 m above the ground) using a Trephor 140 mm long and 5 mm in diameter (Rossi *et al.*, 2006).

All samples were stored and transported in plastic tubes filled with a 70 % ethanol solution to avoid fungal infestation. In the laboratory, transversal, radial and tangential micro-thin sections (50 μm) were prepared with a sliding microtome (type G.S.L.1 light-weight microtome). The transversal sections were prepared from all 20 samples, while radial and tangential thin sections were prepared from a subset of five

samples. The thin sections were stained with a mixture of Astra-blue and Safranin for 3–5 min to discriminate lignified (red) from unlignified (blue) tissues (Schweingruber *et al.*, 2006). The stained thin sections were rinsed with demineralized water and dehydrated with a graded series of ethanol (50 %, 96 % and 100 %). Then, for permanent fixation, the sections were rinsed with xylol and embedded in Canada balsam and dried at 60 °C for 12 h in the oven.

Bark and resin secretory structures

The micro-thin sections were inspected under a light microscope (Leica DM 2500), with a magnification ranging from 12·5 to 400 times. Digital images of the secretory structures present in wood and bark of *B. papyrifera* were made from transversal, tangential and radial sections using a Leica camera (DFC 320) attached to the light microscope.

The bark is described using the terminology of Trockenbrodt (1990) and Junikka (1994). For the purpose of this study, we classified the inner bark into three zones (Figs 1B and 2). The first zone (called intact zone) represents part of the inner bark that is not affected by dilatation and it is found close to the vascular cambium (Fig. 2A). The remaining part of the inner bark which is affected by dilatation is divided into partially dilatated and highly dilatated zones to account for the observed structural variation. The partially dilatated zone (Fig. 2B) is an area adjacent to the intact zone and is less affected by dilatation and has a higher proportion of remnant sclerenchymatic tissues than the highly dilatated zone. The highly dilatated zone (Fig. 2C) is largely dominated by parenchyma.

Data analysis

For the 20 study trees, the diameter of all axial resin canals, as well as the density (number of resin canals per mm^2) of axial resin canals, was measured and calculated from digital images across the inner bark. Functional and non-functional resin canals were discriminated according to the presence or absence of lignification of the cell wall of epithelial cells, indicated by red (= lignified) or blue (= non-lignified) colour. All axial resin canals which did not lose their original shape during the cutting process of thin sections were measured for their internal lumen diameter. All measurements were conducted using the image analysis software ImageJ version 1·44p (http://rsbweb.nih.gov/ij/).

To test for differences in density of resin canals across the three zones of the inner bark, one-way ANOVA accompanied by Tukey *post-hoc* multiple comparison was used. Differences in density of lignified axial resin canals across the different zones of the inner bark were tested using Kruskal–Wallis accompanied with Scheffe's *post-hoc* test. To test for differences in average diameter of axial resin canals among the sample trees, one-way ANOVA was used and, to understand the relationship between density and average diameter of axial resin canals, correlation analysis was used.

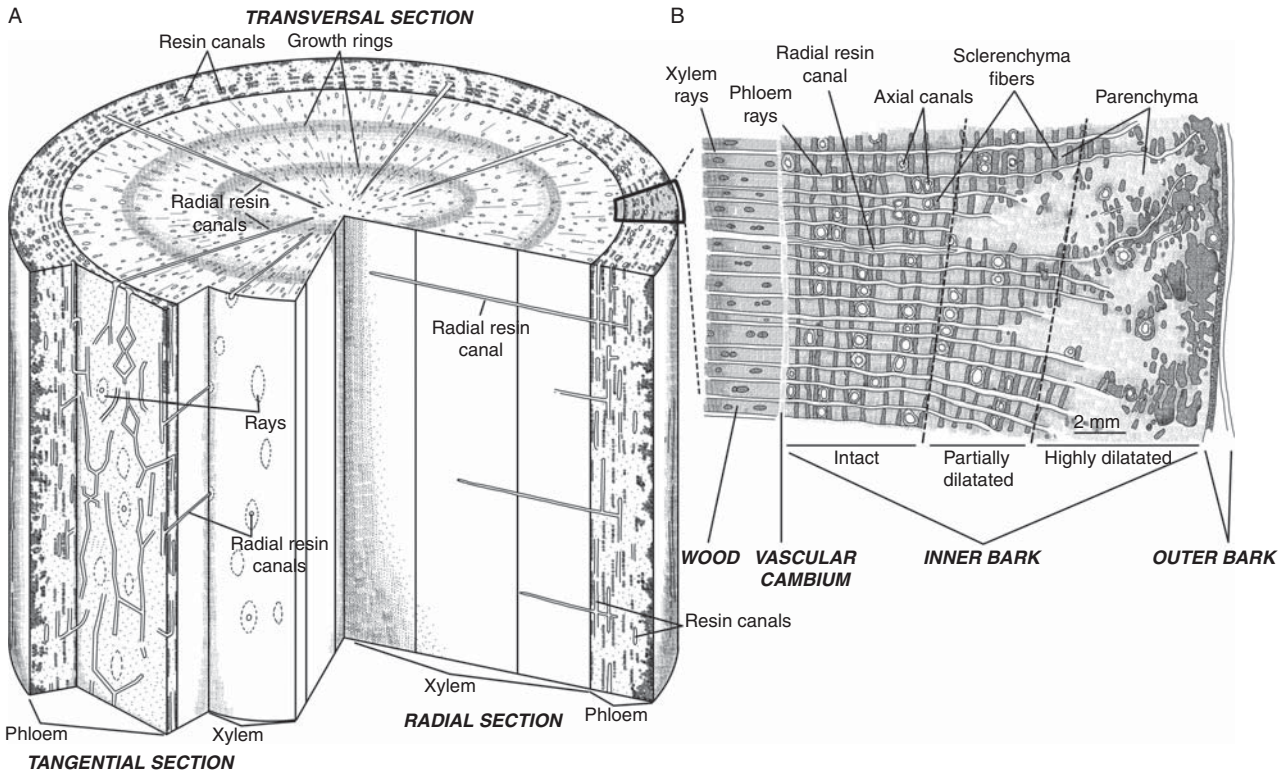

FIG. 1. Microscopic view of the bark and resin secretory structures of a *B. papyrifera* tree: (A) three-dimensional view of resin secretory structure in the xylem and bark (redrawn after Ghosh and Purkayastha, 1960); (B) resin canals and other cell types observed in the bark (note: cell structures of the xylem part are not shown).

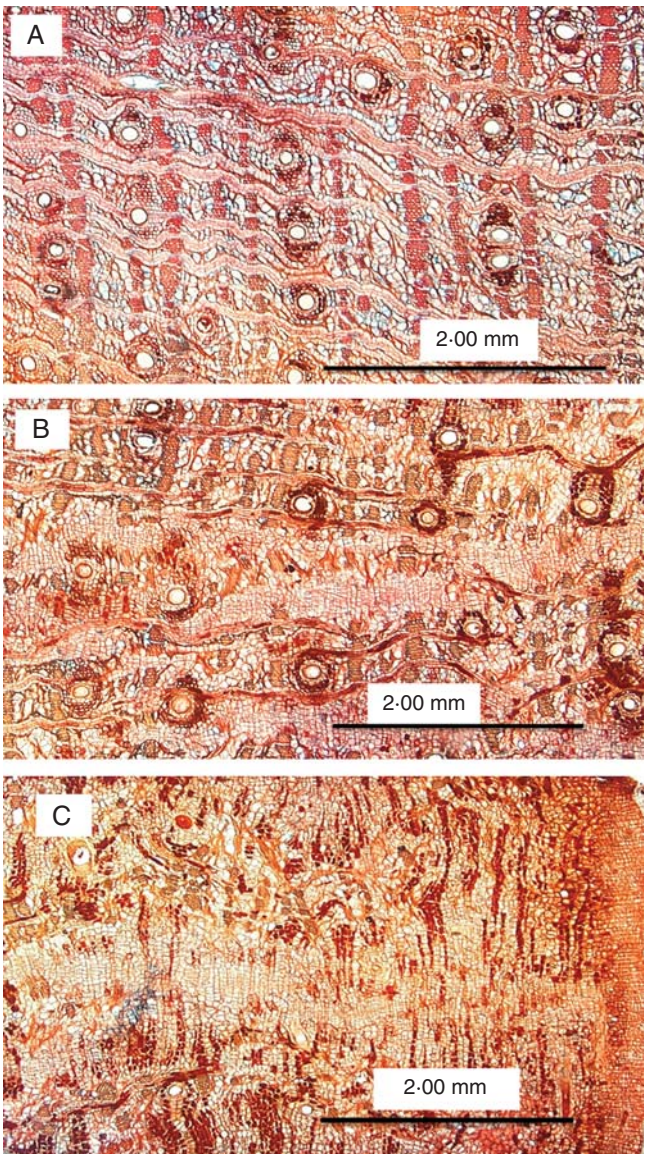

FIG. 2. The three zones of inner bark (transversal section) of *B. papyrifera*: (A) the intact zone, (B) the partially dilatated zone and (C) the highly dilatated zone.

RESULTS

Bark anatomical structure of B. papyrifera

The bark of the studied *B. papyrifera* trees had an average thickness of 17·2 mm (s.d. = 2·3; Table 1), which is about 15 % of the stem radius. It consists of two main layers, the inner bark (17·0 ± 2·3 mm), starting directly after the cambium and the much thinner outer bark (0·2 ± 0·1 mm; Fig. 1B). On the transversal section, the outer bark is seen as one to two layers of multiple cells with thin cell walls. These layers peel off in thin flakes. The inner bark is composed of multiple alternating tangential layers of thick-walled sclerenchyma fibers and thin-walled parenchyma layers (Figs 1B and 2). Sieve plates with companion cells were observed in the parenchyma layers. Phloem rays cut through sclerenchyma and parenchyma layers. Close to the cambium, these alternating layers are well-ordered and characterized as intact. However, the order gets disrupted with increasing distance from the cambium due to dilatation. Dilatation results in wedge-like structures, piercing into the inner bark. This leads to three distinct zones (Fig. 2) in the inner bark: an intact, partially dilatated and highly dilatated zone. Phloem rays are abundant in the intact zone but decline in density towards the dilatation zones (Fig. 2).

TABLE 1. *Characteristics of inner bark of* B. papyrifera *trees (n = 20) from Metema, Ethiopia*

Zones of the inner bark	Radial thickness (mm)				Density of axial resin canals (number mm^{-2})			
	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max.
Intact	6·6	1·8	3·8	10·5	1·0	0·3	0·4	1·5
Partially dilatated	4·7	1·5	2·5	8·3	0·8	0·2	0·4	1·2
Highly dilatated	5·7	2·5	1·2	9·8	0·6	0·2	0·3	1·1
Total inner bark	17·0	2·3	10·8	19·8	0·8	0·2	0·5	1·1

Distinction is made between intact, partially dilatated and highly dilatated parts, encountered in radial direction from vascular cambium to outer bark. All measurements are taken from transversal sections of the bark.
s.d., Standard deviation; Min, Minimum; Max, Maximum.

Resin secretory structures of B. papyrifera

Resin secretory structures of *B. papyrifera* occur predominantly in the inner bark as axial and radial resin canals. The wood contains only a few radial resin canals, which are embedded in the rays (Fig. 1A, B). These canals continue into the inner bark through phloem rays (Fig. 3A) where they merge into a three-dimensional network of axial and radial resin canals. No other resin secretory structures such as resin pockets were observed on transversal, radial nor tangential sections of wood and bark samples. On the cross-section, axial resin canals are visible within the multi-layer sheets of axial parenchyma cells arranged in tangential rows (Fig. 2A). Axial canals are much more abundant than radial canals. Both axial and radial resin canals are surrounded with epithelial cells. In the intact zone of the inner bark, epithelial cells around axial resin canals are exclusively non-lignified (Fig. 3C), while epithelial cells around some of the axial resin canals in the dilatated areas are lignified (Fig. 3D).

Tangential sections of the intact zone of the inner bark show that axial resin canals are mutually connected (Fig. 1A). These canals split up and join neighbouring axial resin canals again (anastomosis), thereby forming tangential connections (Fig. 3B). The elongated radial resin canals are connected to multiple axial resin canals (Fig. 1A) completing the three-dimensional network. In the dilatated parts of the inner bark this network gets increasingly disrupted.

Distribution, density and size of axial resin canals in the inner bark

The intact, the partially dilatated and the highly dilatated zones, respectively, cover an average of 39 %, 28 % and 33

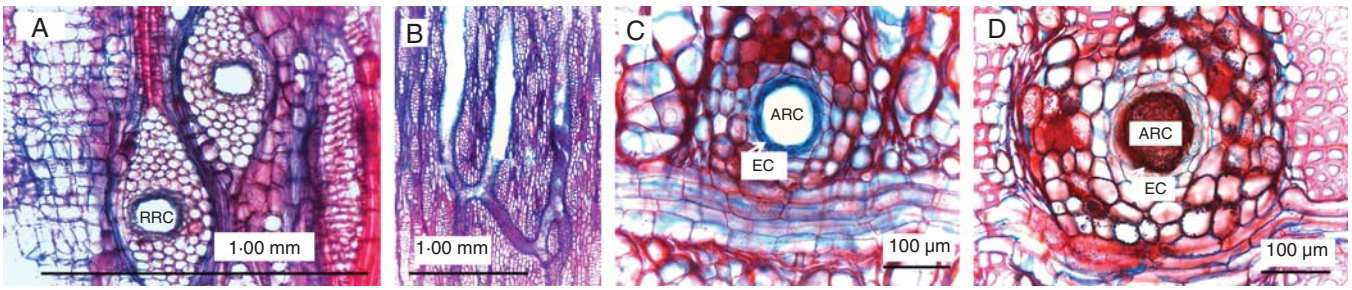

FIG. 3. Axial and radial resin canals in the bark of *B. papyrifera*: (A) radial resin canals (RRC) embedded in rays (tangential section); (B) anastomosis of axial resin canals in the inner bark (tangential section); (C) transversal view of axial resin canal (ARC) surrounded by non-lignified epithelial cells (EC, arrow) and other parenchyma cells (indicated by blue stain = living) and (D) axial resin canal (ARC) surrounded by lignified (dead) epithelial cells (EC, arrow) and other parenchyma cells (stained red = dead).

% of the thickness of the inner bark (Table 1). On average, there are 0·8 axial resin canals per mm^2 (s.d. = 0·2) in the inner bark. However, the density of axial resin canals significantly decreases from the intact towards the highly dilatated zone (ANOVA, $F_{2,57} = 14{\cdot}63$, $P < 0{\cdot}001$; Fig. 4A and Table 1). Lignified axial resin canals which account for 4 % of the average density of axial resin canals exclusively occur in the dilatated zones. The highly dilatated zone contains most lignified resin canals (Kruskal–Wallis, d.f. = 2, $\chi^2 = 34{\cdot}626$, $P < 0{\cdot}001$; Fig. 4B).

The average diameter of all individual axial resin canals measured from 20 trees ranges between 30 and 232 µm with an average of 113 µm (s.d. = 30; $n = 1707$ axial resin canals). The diameter of resin canals significantly differs between trees (ANOVA, $F_{19,1687} = 25{\cdot}598$, $P < 0{\cdot}001$). Moreover, the studied trees showed a trade-off between density and average diameter of axial resin canals (Pearson correlation, $n = 20$, $r = -0{\cdot}625$, $P < 0{\cdot}01$; Fig. 5).

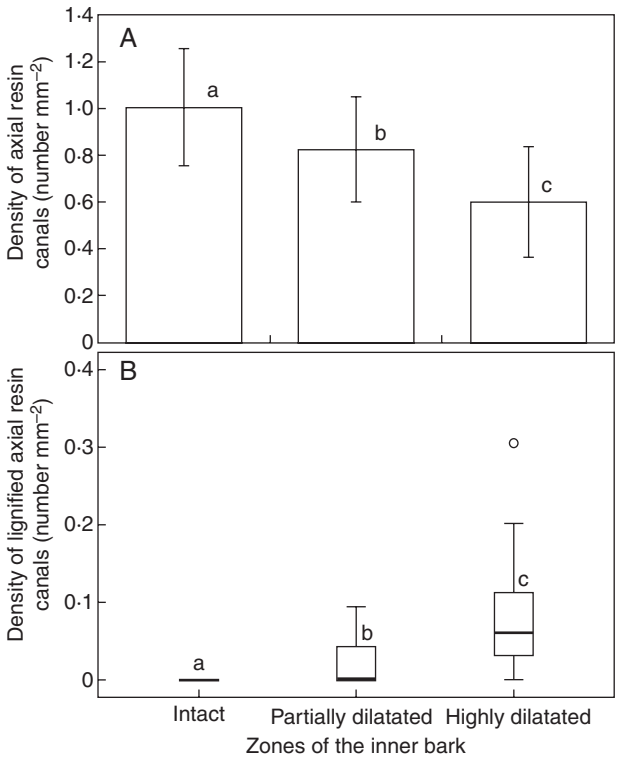

FIG. 4. Resin canal density in the three different zones of the inner bark of *B. papyrifera*. (A) Density of all lignified and unlignified axial resin canals (error bars = ± s.d.) and (B) a box plot of density of lignified axial resin canals. The circle above the 'Highly dilatated' box indicates an outlier value. Different letters indicate significant differences, using $P < 0{\cdot}05$ [Tukey test (A) and Scheffe test (B), $n = 20$]. Note difference in scales of *y*-axes.

DISCUSSION

Resin secretory structures of B. papyrifera

As expected, resin secretory structures of *B. papyrifera* are predominantly found in the bark. Axial and radial resin canals form a three-dimensional network in the intact zone. In this relatively small zone, which accounts for less than half of the thickness of the inner bark, the network of resin canals is mostly intact and so is most likely to be functional for short- and long-distance resin transport. Radial resin canals connect the canal network of the bark to the wood. This hints to the possibility of radial transport of resin between wood and bark. Previous studies showed similar results for *B. serrata* from India (Ghosh and Purkayastha, 1960) and interconnected canals are also reported for Pinaceae (Bosshard and Hug, 1980; LaPasha and Wheeler, 1990; Lewinsohn *et al.*, 1990) and Araliaceae (Kolalite *et al.*, 2003).

With increasing distance from the cambium, the density of axial resin canals decreases strongly. This decrease is caused by dilatation occurring due to increasing tangential strain as trees grow in circumference (Trockenbrodt, 1990; Kolalite *et al.*, 2003). The dilatation is realized by the production of new parenchyma cells that are formed by phloem parenchyma cells which regain meristematic status (Kolalite *et al.*, 2003; Lev-Yadun, 2011). Resin canals surrounded by lignified epithelium cells occur more frequently within the dilatated zones of the inner bark and can be taken as an indicator of non-functionality (Oven and Torell, 1999). Lignification of cells around resin canals is possibly related to the rupture of the secretory system as a consequence of dilatation (Bannan, 1936). However, also without evidence from lignification, it can be assumed that disorder of cells, both in partly and highly dilatated parts of the inner bark, will result in disruption of the network of resin secretory structures and disable – at least – long-distant transport of resin in these parts.

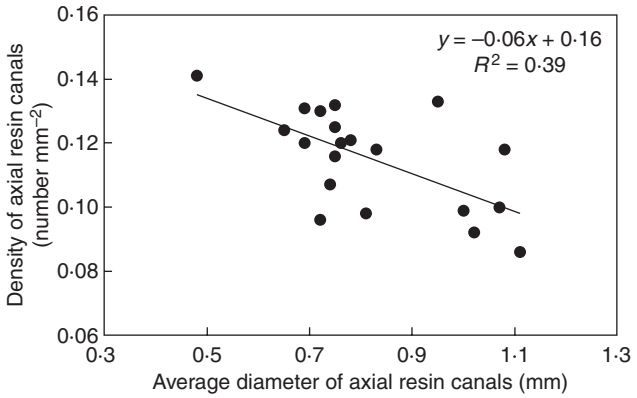

FIG. 5. Relationship between resin canal diameter and density in 20 *B. papyrifera* trees. Circles represent individual trees, and the scores represent density (number mm^{-2}) and average diameter (mm) of axial resin canals for each tree.

Implications for tapping

This study showed that the diameter of resin canals varies among studied trees of the same diameter class. Roosner and Hannup (2004) indicated that resin canal traits are strongly controlled by genetic variations. For spruce and pine, the diameter of resin canals is an important resin canal trait which is related to resin yield (Baier *et al.*, 2002). Hence, differences in diameter of resin canals might partly contribute to observed differences in frankincense yield among trees of the same diameter class as described for *B. papyrifera* from our study area (Tadesse *et al.*, 2004; Eshete *et al.*, 2012*a*).

Previous studies showed that yield of frankincense per tree increases during the first five to seven tapping rounds and then declines when more tapping rounds are added later in the dry season (Tilahun *et al.*, 2011; Eshete *et al.*, 2012*a*). In the context of the results of this study, this initial increase in resin yield can be related to the fact that in the case of successively deeper cuts into the bark, the tapping proceeds into the inner zones with a high density of resin canals and an intact three-dimensional network of functional resin canals. The decline in yield after seven rounds of tapping (Eshete *et al.*, 2012*a*) suggests depletion of resin as it is drained through the well-structured network in the intact part of the inner bark. The strong reduction of resin yield towards the end of the tapping season most likely indicates depletion of the trees' carbon stock (Mengistu *et al.*, 2012).

The anastomoses of resin canals facilitate long-distance resin transport and, presumably, work like a draining system in case of wounding, here specifically tapping. This may lead to a conclusion that larger wounds might not necessarily yield more resin while introducing more stress to the tree as it has to close the wound by production of wound tissue and wood to overgrow the wound (Shigo, 1984; Pearce, 1996). This is supported by results from Tadesse *et al.* (2004) who showed that enlarging the size of wounds for tapping *B. papyrifera* trees does not pay off in resin yield. Other results showing that resin yield per tree initially increases, then levels off and starts to decline with increasing number of tapping spots (Tilahun *et al.*, 2011; Eshete *et al.*, 2012*a*) can also be explained by the findings of this study. The decline in resin yield beyond a certain number of tapping spots may occur because wounds drain resin from the same pool.

The presence of interconnected canals (Raffa and Berryman, 1982; Lewinsohn *et al.*, 1990), coupled with our observation of immediate flow of resin from the bark when the tree is wounded, indicate that frankincense is present in the secretory system as a preformed resin. Therefore, it could be beneficial to drain all the preformed resin with a first deep cut into the intact part of the inner bark, i.e. to the depth that is usually reached during the tapping round that yields the maximum yield (i.e. 7th tapping round, Eshete *et al.*, 2012*a*). Although the flow of resin will eventually be blocked by drying frankincense on the wound surface and the wound has to be re-opened to drain all preformed resin, the amount of labour required for production of frankincense could be reduced. This strategy would moreover be less harmful for the tree than initiation of multiple wounds to drain the same pool. The consequences of such one big deeper cut for frankincense yield as well as the related physiological processes require further research. We recommend additional specific experiments on different levels of cutting depths and on optimum distances between tapping wounds based on tree size.

From earlier studies, it is evident that tapping increases adult mortality (Varghese and Ticktin, 2008), reduces reproductive effort (Rijkers *et al.*, 2006; Mengistu *et al.*, 2012), reduces growth of trees (Silpi *et al.*, 2006; Mengistu, 2011) and exposes the trees to insect attack (Herms and Mattson, 1992; Abiyu *et al.*, 2010). The current decline in populations of *B. papyrifera* across large areas in Ethiopia (Groenendijk *et al.*, 2012; Eshete, 2011) and Eritrea (Ogbazghi *et al.*, 2006) can partly be attributed to over-tapping (Abiyu *et al.*, 2010; Mengistu, 2011). This indicates that the current tapping strategies need to be improved. One of the strategies under discussion is reducing the number of tapping rounds per season and reducing the number of tapping spots per tree (Abiyu *et al.*, 2010; Eshete *et al.*, 2012*a*; Mengistu *et al.*, 2012). Our findings on the bark anatomy and distribution and architecture of resin secretory structures of *B. papyrifera* will stimulate new experiments aimed at improving tapping techniques. This contributes to the development of a more sustainable frankincense production that enhances the contribution of frankincense to rural livelihoods and the national economy.

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